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THE MEASUREMENT OF THE INTENSITY OF INBREEDING

CONTENTS.

PAGE

Preliminary Definitions 124

The Measurement of the Degree of Inbreeding 125

The Relation of Coefficients of Inbreeding to the Hereditary Constitution of the Individual..... 135

Concluding Remarks 137

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BULLETIN No. 215.

THE MEASUREMENT OF THE INTENSITY OF INBREEDING.[1]

RAYMOND PEARL.

The effect of inbreeding on the progeny is a much discussed problem of theoretical biology and of practical breeding. It has been alternately maintained, on the one hand, that inbreeding is the most pernicious and destructive procedure which could be followed by the breeder, and on the other hand, that without its powerful aid most of what the breeder has accomplished in the past could not have been gained and that it offers the chief hope for further advancement in the future. While there is now, among animal breeders at least, a more widespread tendency than was formerly the case towards the opinion that inbreeding *per se* is not a surely harmful thing, nevertheless this opinion is by no means universally held and in any case does not rest upon a definite and well-organized body of evidence. Aside from a relatively small amount of definite experimental data one's judgment in the matter (so far as it is not wholly speculative) is finally formed on the basis of his *interpretation* of the vast accumulation of material comprised in the recorded experience of the breeders of registered (pedigreed) livestock.

[1]This bulletin is essentially an abstract (with some new material—see p. 134) of a more extended technical discussion of the subject published, with the title "A Contribution towards an Analysis of the Problem of Inbreeding," in the American Naturalist (Vol. XLVII, 1913). The complete paper contains illustrative pedigrees and examples of the calculation of coefficients of inbreeding, together with a more detailed discussion of the theoretical significance of these coefficients. Anyone wishing to make use of these coefficients of inbreeding should consult the original paper, in addition to this abstract. The paper referred to is *not* available for general distribution by the Maine Agricultural Experiment Station. Recourse must be had by those wishing to examine it to the files of the American Naturalist, a journal available in many of the larger public libraries, or by purchase at a nominal cost from the publishers.

In order that progress may be made in the analysis of this important problem of inbreeding there is a fundamental need which must first be met. This is the need for an appropriate and valid method of pedigree analysis, which possesses generality, and can on that account be depended on to give comparable results when applied to two (or more) different pedigrees. Specifically, there seems not to have been worked out any *adequate general method of measuring quantitatively the degree of inbreeding which is exhibited in a particular pedigree.* Without such a measure it is clearly impossible to proceed far in the analysis of inbreeding.

It is the purpose of the paper of which this is an abstract to present a method for measuring, and expressing numerically in the form of a coefficient, the degree of inbreeding which exists in any particular case, and to show by illustrations the manner in which these coefficients may be computed. It is shown that the method is (a) *unique,* in the sense that the value obtained in any particular instance can only be affected by the degree or amount of inbreeding which has been practiced in the line of descent under consideration, and (b) *general,* in the sense that it is equally applicable to all pedigrees and to all degrees and types of inbreeding.

Preliminary Definitions.

In attempting any general analysis of the problem of inbreeding from the theoretical standpoint one is confronted with the necessity for a definition of inbreeding, which shall be at once precise and general, that is, such as to include all of the most diverse ways in which this sort of breeding may be practised.

Leaving aside for the moment all consideration of details as to *how* a particular piece of inbreeding may be brought about is to be found the concept of a *narrowing* of the network of descent as a result of mating together individuals genetically *related* to one another in some degree. Let us take this as our basic concept of inbreeding. It means that the number of potentially *different* germ-to-germ lines, or "blood-lines" concentrated in a given individual animal is *fewer* if the individual is inbred than if it is not. In other words, *the inbred individual possesses fewer different ancestors in some particular generation or generations than the maximum possible number for that*

generation or generations. This appears to be the most general form in which the concept of inbreeding may be expressed. In whatever way the mating of relatives is accomplished, or whatever the degree of relationship of the individuals mated together, the case in last analysis comes back to the above statement, namely that there are actually in the pedigree of the inbred individual fewer *different* ancestors in some particular generation or generations than the maximum possible number.

The Measurement of the Degree of Inbreeding.

This brings us to a consideration of a practical and general measure of the degree of inbreeding exhibited in a particular pedigree. This problem has been attacked by a number of other investigators, but so far as I have been able to learn, all previous measures have been modifications in one form or another of the scheme of Lehndorff. All systems based on the number of "free generations" alone, as in Lehndorff's, do not furnish a precise or reliable measure of the real intensity of inbreeding. The essential reason for this failure, stated baldly, is that they do not take account of the composition of the generation to which the "common ancestor" of an inbred pair belongs.

In developing a general measure of the intensity of inbreeding we may well start from the conception set forth in the preceding section, namely that the inbred individual possesses fewer different ancestors than the maximum possible number. Besides this factor account must be taken of the generation or generations in which the reduced number of different ancestors is found, and the extent to which these generations are removed (in the sense of Lehndorff mentioned above) from the individual or generation under consideration. In other words the two factors which must be included in a general measure of the intensity of inbreeding are (a) the *amount* of ancestral reduction in successively earlier generations, and (b) the *rate* of this reduction ever any specified number of generations.

Both of these demands are met by taking as a measure of the intensity of inbreeding in any generation the proportionate degree to which the actually existent number of different ancestral individuals fails to reach the maximum possible number,

and by specifying the location in the series of the generation under discussion.

This statement is amplified and made more precise in the following propositions.

1. The production of the individual must be the point of departure in any analytical consideration of inbreeding, leading towards its measurement. That is, the question to which one wants an answer is: What degree of inbreeding was involved in the production of this particular animal?

2. It is therefore necessary practically to *start* with the individual and work *backwards* into the ancestry in measuring inbreeding, rather than to start back in the ancestry and work down towards the individual.

3. In the genetic passage from the $n+1$'th generation to the n'th, or in other words the contribution of the matings of the $n+1$'th generation to the total amount of inbreeding involved in the production of an individual, the degree of inbreeding involved will be measured by the expression

$$Z_n = \frac{100\,(p_{n+1} - q_{n+1})}{p_{n+1}} \qquad \text{(i)}$$

where p_{n+1} denotes the maximum possible number of different individuals involved in the matings of the $n+1$ generation, q_{n+1} the *actual* number of different individuals involved in these matings. Zn may be called a *coefficient of inbreeding*. If the value of Z for successive generations in the ancestral series be plotted to the generation number as a base, the points so obtained will form a curve which may be designated as the *curve of inbreeding*.

It will be noted that the coefficient of inbreeding Z is the percentage of the difference between the maximum possible number of ancestors in a given generation and the actual number realized in the former. The coefficient may have any value between 0 and 100. When there is no breeding of relatives whatever (that is, in the entire absence of inbreeding) its value for each generation is 0. As the intensity of the inbreeding increases the value of the coefficient rises.

4. The above measure of inbreeding has to do solely with the *relationship* aspect of the problem. It has nothing whatever

to do *directly* with the gametic or zygotic constitution of individuals.

5. Since the only possible infallible criterion of relationship between individuals is common ancestry in some *earlier* generation, we are led to the practical rule, in measuring the degree of inbreeding in a pedigree, *to regard all different individuals as entirely unrelated until the contrary is proved by the finding of a common ancestor.* This no doubt appears at this stage of the discussion as an exceedingly obvious truism. The reader is urged to accept it as such, and hold fast to it, because it will help him over some apparent paradoxes later.

The method of calculating coefficients of inbreeding, and their real significance will be made much clearer by the consideration of illustrative examples of their application. To these we may therefore turn.

The Calculation of Coefficients of Inbreeding.

We may first consider some simple hypothetical pedigrees,

Pedigree Table I. (Hypothetical).

To illustrate the Breeding of Brother × Sister, out of Brother × Sister, Continued for a Series of Generations.

<table>
<tr><td rowspan="8">x</td><td rowspan="4">a</td><td rowspan="2">c</td><td>e</td><td>g</td></tr>
<tr><td>h</td></tr>
<tr><td>f</td><td>g</td></tr>
<tr><td>h</td></tr>
<tr><td rowspan="2">d</td><td>e</td><td>g</td></tr>
<tr><td>h</td></tr>
<tr><td>f</td><td>g</td></tr>
<tr><td>h</td></tr>
<tr><td rowspan="8">b</td><td rowspan="4">c</td><td>e</td><td>g</td></tr>
<tr><td>h</td></tr>
<tr><td>f</td><td>g</td></tr>
<tr><td>h</td></tr>
<tr><td rowspan="4">d</td><td rowspan="2">e</td><td>g</td></tr>
<tr><td>h</td></tr>
<tr><td rowspan="2">f</td><td>g</td></tr>
<tr><td>h</td></tr>
</table>

before attacking the more complicated ones actually realized in stock-breeding.

ILLUSTRATION I. CONTINUED BROTHER × SISTER BREEDING.

Let us begin with the most extreme type of inbreeding possible, namely the mating of brother with sister for a series of generations. Pedigree Table I gives the pedigree of an individual so bred.

Let us now proceed to calculation of the coefficients of inbreeding Z_0, Z_1, Z_2, and Z_3. For Z_0 we have

$$p=2.$$
$$q=2,$$

whence $$Z_0 = \frac{100\ (0)}{2} = 0$$

In the same way $$Z_1 = \frac{100\ (4-2)}{2} = 50$$

$$Z_2 = \frac{100\ (8-2)}{8} = 75$$

$$Z_3 = \frac{100\ (16-2)}{16} = 87.5$$

These results may be expressed verbally in the following way: In the last two ancestral generations x is 50 per cent inbred; in the last three generations it is 75 percent inbred; and in the last four generations it is 87.5 per cent inbred.

This pedigree table and the constants will repay further consideration, since the case is a limiting one. With the table at hand it is possible to grasp a little more clearly the precise biological meaning of the coefficients of inbreeding. Thus it is seen that what the value of $Z_1=50$ really signifies is that because the individual a and b were brother and sister the number of different ancestors which x can possibly have in any ancestral generation cannot be *more* than 50 percent of the total number theoretically possible for the generation. That is, x's sire and dam having been brother and sister means that x cannot have more than 2049 different great-great-great-great-great-great-great-great-great-great-grandparents, instead of the pos-

sible 4096. He may have had fewer than 2049, but $Z_1=50$ tells us that he could not have had more. Similarly $Z_2=75$ indicates that since *c* and *d*, the grand-sire and grand-dam of *x* were brother and sister, *x* cannot have in any ancestral generation more than 25 percent of the theoretically possible number of ancestors for that generation. And so on for the other values of *Z*.

In the limiting case of the closest inbreeding possible the successive Z's will have the values given in the following table.

TABLE 1.

Values of the Successive Coefficients of Inbreeding (Z_0 to Z_{15}) in the Case of the Most Intense Inbreeding Possible (Brother × Sister Out of Brother × Sister Continued).

Coefficient of Inbreeding.	Ancestral Generations Included.	Numerical Value of Coefficient.
Z_0	1	0
Z_1	2	50
Z_2	3	75
Z_3	4	87.5
Z_4	5	93.8
Z_5	6	96.9
Z_6	7	98.4
Z_7	8	99.2
Z_8	9	99.6
Z_9	10	99.8
Z_{10}	11	99.9
Z_{11}	12	99.95
Z_{12}	13	99.98
Z_{13}	14	99.99
Z_{14}	15	99.994
Z_{15}	16	99.997

From this table it is apparent that while the narrowing or exclusion of the possible different source lines of descent proceeds very rapidly in the first few generations of brother × sister breeding, only relatively little change is made by further generations of this sort of breeding. Thus in seven generations of brother × sister breeding all but about 1 1-2 percent of the potentially different ancestral "blood-lines" will have been eliminated.

The values of the *Z*'s in Table 1 are maxima: No particular coefficient of inbreeding can have a higher value than that given in the table. It is not possible, for example, so to breed any domestic animal that its pedigree on analysis will give $Z_3 >$

87.5. If therefore, the coefficients of Table 1 are plotted the result will be the maximum limiting *curve* of inbreeding.

Illustration II. Parent × Offspring Breeding.

The next illustration of the application of coefficients of inbreeding will be the general case of back-crossing, that is the mating of parent × offspring.

The values of the successive coefficients for parent × offspring breeding for 16 ancestral generations are given in Table 2.

Table 2.

Values of the Successive Coefficients of Inbreeding in the Case of Continued Parent × Offspring Mating.

Coefficient of Inbreeding.	Ancestral Generations Included.	Numerical Value of Coefficient.
Z_0	1	0
Z_1	2	25
Z_2	3	50
Z_3	4	68.75
Z_4	5	81.25
Z_5	6	89.06
Z_6	7	93.75
Z_7	8	96.48
Z_8	9	98.05
Z_9	10	98.93
Z_{10}	11	99.41
Z_{11}	12	99.68
Z_{12}	13	99.83
Z_{13}	14	99.91
Z_{14}	15	99.95
Z_{15}	16	99.97

By comparison of this table with Table 1 it is evident that while the increase in intensity of inbreeding is not so rapid in the first few ancestral generations by this parent × offspring type of breeding as with the brother × sister type, by the time the 10th ancestral generation is reached the values are, for practical purposes, the same.

Illustration III. The Pedigree of the Jersey Cow, Bess Weaver (155121).*

Leaving now the hypothetical cases we may consider some pedigrees of actually existing animals. For a first illustration of this sort the Jersey cow Bess Weaver may be taken. Her pedigree through four ancestral generations is shown in pedigree table II.

PEDIGREE TABLE II.

Sex ♀	♂			
Bess Weaver No. 155121	No. 53598 Davy Stoke Pogis	No. 35913 ♂ Sisera's Stoke Pogis	No. 26271 ♂ Juno's Stoke Pogis	No. 14207 ♂ Alphea's Stoke Pogis
				No. 14436 ♀ Carlo's Juno
			No. 37346 ♀ Sisera	No. 18811 ♂ Duchess Stoke Pogis
				No. 6246 ♀ Edith Darby
		No. 79860 ♀ Baltimore	No. 19350 ♂ Patrick Fawkes	No. 10469 ♂ Regal Koffee
				No. 21574 ♀ Kermesse
			No. 17900 ♀ Avoca 2nd	No. 3286 ♂ Champion's Son
				No. 17769 ♀ Avoca
	♀	No. 35913 ♂ ⊕ Sisera's Stoke Pogis	No. 26271 ♂ × Juno's Stoke Pogis	No. 14207 ♂ × Alphea's Stoke Pogis
				No. 14436 ♀ × Carlo's Juno
			No. 87346 ♀ × Sisera	No. 18811 ♂ × Duchess Stoke Pogis
				No. 6246 ♀ × Edith Darby
	No. 126629 Peg Weaver	No. 126626 ♀ Kate Weaver	No. 36382 ♂ General Kelly	No. 19350 ♂ ⊗ Patrick Fawkes
				No. 95606 ♀ ⊕ Balm
			No. 95606 ♀ Balm	No. 7056 ♂ America's Champion
				No. 95605 ♀ Maid of Gilead 2nd

In the twelfth ancestral generation the theoretically possible number of different ancestors is 4096. In a relatively long pedigree, such as arises in dealing with registered cattle, it would obviously be an extremely tedious business to determine the value of q by direct counting, as has been done in the preceding simpler illustrations. The calculation of the coefficients of inbreeding may be greatly simplified in the case of long pedigrees by a system of counting which makes the *line of*

* The illustrations from actual pedigrees used in this abstract are not the same as those used in the complete paper. The two illustrations here given are chosen because of their probably greater interest to the Station's constituency.

descent the unit rather than the individual. This system is used in the above pedigree as an illustration of method, although only 4 ancestral generations are here considered. While each individual animal which is eliminated because of previous appearances in a lower ancestral generation is marked with an *X*, those at the apex of a line of descent are marked with a cross within a circle. These latter are all that need to be counted directly. Their elimination automatically eliminates their own ancestors. Thus the bull Sisera's Stoke Pogis first appears in the second ancestral generation as the sire of Davy Stoke Pogis. He next appears (here marked with a cross within a circle) in the same generation as the sire of Peg Weaver. He will, by the general rule for coefficients of inbreeding, not be counted as a "different" ancestor the second time in this generation. But this automatically eliminates his two parents in the third ancestral generation, his four grandparents in the fourth generation, and so on until in the twelfth generation 1024 ancestors of Sisera's Stoke Pogis will be so eliminated. The same consideration applies in every other like case.

Practically then the method of dealing with a pedigree of this sort is first to go through and indicate in a distinctive way every *primary** reappearance of individuals. Then form a table on the plan of Table 3, the character of which is so obvious as not to need detailed explanation.

This table is to be read in the following way: Because of the reappearance of Sisera's Stoke Pogis in the 2nd ancestral generation Bess Weaver has 1 fewer ancestors in that generation than she would have had in the entire absence of inbreeding: 2 fewer in the 3rd generation and so on. The totals of the columns of this table are the values, for each generation, of

$$f_{n+1} - y_{n+1}$$

* By "primary" reappearance in the pedigree is meant a reappearance as the sire or dam of an individual which has not itself appeared before in the lower ancestral generations. Thus Patrick Fawkes makes a *primary* reappearance in the fourth ancestral generation as the sire of General Kelly, a bull which is not found in any generation below the third.

TABLE 3.

Working Table Used in Calculating the Coefficients of inbreeding for Pedigree Table II.

ANIMAL.	ANCESTRAL GENERATION.		
	2.	3.	4.
Sisera's Stoke Pogis	1	2	4
Patrick Fawkes	–	–	1
Balm	–	–	1
Totals	1	2	6

in (i). These totals, multiplied by 100, have then merely to be divided by p_{n+1} in order to obtain the successive Z's. The whole operation may be very quickly carried out. It is not necessary, in fact, to fill out the whole of the later columns of the table, the entries may be cumulated.

For the present pedigree we have

$$Z_0 = 0, \text{ as always*}$$

$$Z_1 = \frac{100\ (1)}{4} = 25\%$$

$$Z_2 = \frac{100\ (2)}{8} = 25\%$$

$$Z_3 = \frac{100\ (6)}{16} = 37.5\%$$

From these values it is seen that in the first four ancestral generations the cow Bess Weaver is 37.5 percent inbred. This is a perfectly definite figure, directly comparable with similar constants for other animals. Of course, if we were to go back more generations we should find Bess Weaver still more inbred, that is, the coefficients would grow larger with each case of the mating of relatives. Since the case is cited here merely for illustration of method, four generations only are considered.

* The apparent paradox implied in the fact that Z_0 must always be zero, or in other words that in the first ancestral generation, considered *alone*, there is no inbreeding will be cleared up, if it strikes the reader as paradoxical, by a reconsideration of the general principle numbered 5 on p. 127. The point of course is that it is impossible to say whether the parents are or are not related to one another until something is known of *their* parentage, or in other words, until a *second* ancestral generation is considered.

Illustration IV. The Pedigree of the Jersey Cow, Figgis 20th of Hood Farm (190306).

Figgis 20th of Hood Farm (190306) is a cow which, in official test for advanced registry, produced as a two year old 437 lbs. 14.4 oz. butter fat. This is a high record. The complete pedigree of this animal has been worked out for 12 ancestral generations, and the coefficients of inbreeding calculated. Twelve generations cover practically the whole of the known pedigree of this cow. On account of its great length it is impossible in the space here available to reproduce this pedigree. Nor is it necessary. The inbreeding coefficients in a quarter of a page give more clear and definite information regarding the amount of inbreeding practised in the breeding of Figgis 20th than could any visual inspection of the pedigree itself. Furthermore the list of names in Table 4 shows just what animals appear more than once in the pedigree, and how frequent are their reappearances.

Table 4 is precisely the same sort of table for Figgis 20th that Table 3 is for Bess Weaver.

In dealing with this and all other pedigrees it is assumed, in the absence of information on the point and the impossibility of acquiring any, that any imported animal for which there is no further pedigree, was not inbred to any degree whatsoever. This is probably not often strictly true, but, on the other hand, some assumption must be made, and this puts all individuals on an equal footing. It is in accord with the principle laid down earlier (p. 127) that in pedigree analysis all individuals must be considered to be unrelated until the contrary is proved by the evidence of their ancestry. After all, the only thing we can possibly measure is the inbreeding shown in the *recorded* pedigree. All that happened prior to the beginning of the record must be a matter of assumption. The *same* assumption should, however, be made for all cases. What this assumption really means practically is that, in all cases of analysis of actual pedigrees, which are bound after a time to come to an end, the values of the coefficients of inbreeding obtained are *lower limiting values*. They signify that the intensity of inbreeding in a particular case could not have been *less* than that indicated; it

may have been more. Whether it was or not is not a question open to scientific determination but only to speculation.

From this table the following coefficients of inbreeding for Figgis 20th are easily calculated.

$Z_0 = 0$
$Z_1 = 0$
$Z_2 = 12.50$ percent
$Z_3 = 12.50$ "
$Z_4 = 21.88$ "
$Z_5 = 25.00$ "
$Z_6 = 32.03$ "
$Z_7 = 35.94$ "
$Z_8 = 37.30$ "
$Z_9 = 37.99$ "
$Z_{10} = 38.48$ "
$Z_{11} = 38.57$ "

These coefficients show that Figgis 20th was at least 38 1-2 percent inbred. That is, she had rather less than two-thirds as many different ancestors as she would have had in the event of no inbreeding whatever. It is further clear that most of this inbreeding took place in the fourth and earlier ancestral generations, chiefly in the fourth, fifth, and sixth generations.

Comparing Figgis 20th with Bess Weaver we see that the latter is practically as much inbred in the first 4 ancestral generations as Figgis 20th is in the first 12. Considering in each case only the first four ancestral generations the figures show that, within these generations, Bess Weaver is exactly 3 times more intensely inbred than Figgis 20th.

The Relation of Coefficients of Inbreeding to the Hereditary Constitution of the Individual.

What, if any is the relation of coefficients of inbreeding to the zygotic constitution (i. e., the hereditary make-up) of the individual? Do the coefficients tell us anything regarding this matter? A little consideration shows that they do. The successive coefficients of inbreeding indicate the rate and degree to which the possible number of *different* hereditary unit factors present in the ancestry is subsequently reduced as a result of inbreeding. They give no indication of the condition in which the *remaining* factors are present (i. e., whether in homogygous

Table 4.

Working Table for Calculating the Coefficients of Inbreeding of Figgis 20th.

Animal.	Ancestral Generations.									
	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
Sophie's Tormentor	1	2	4	8	16	32	64	128	256	512
Ida's Stoke Pogis	–	–	1	2	4	8	16	32	64	128
Catono	–	–	1	2	4	8	16	32	64	128
Rosabelle Hudson	–	–	1	2	4	8	16	32	64	128
Khedive	–	–	–	1	2	4	8	16	32	64
Young Fancy	–	–	–	1	2	4	8	16	32	64
Stoke Pogis 3rd	–	–	–	–	1	2	4	8	16	32
Marjoram	–	–	–	–	1	2	4	8	16	32
Lord Lisgar	–	–	–	–	1	2	4	8	16	32
Tormentor	–	–	–	–	1	2	4	8	16	32
Oonan	–	–	–	–	1	2	4	8	16	32
Landseer	–	–	–	–	1	2	4	8	16	32
Optimus	–	–	–	–	1	2	4	8	16	32
Jersey Bull of Scituate	–	–	–	–	1	2	4	8	16	32
Hebe	–	–	–	–	1	2	4	8	16	32
Victor Hugo	–	–	–	–	–	1	2	4	8	16
Lord Lisgar	–	–	–	–	–	1	2	4	8	16
Victor Hugo	–	–	–	–	–	1	2	4	8	16
Roxbury	–	–	–	–	–	1	2	4	8	16
Gen'l Scott	–	–	–	–	–	1	2	4	8	16
Europa	–	–	–	–	–	1	2	4	8	16
Europa	–	–	–	–	–	1	2	4	8	16
Mollie	–	–	–	–	–	1	2	4	8	16
Sir Charles	–	–	–	–	–	1	2	4	8	16
Pharos	–	–	–	–	–	1	2	4	8	16
Clement	–	–	–	–	–	–	1	2	4	8
Hebe	–	–	–	–	–	–	1	2	4	8
Lady Mary	–	–	–	–	–	–	1	2	4	8
Fancy	–	–	–	–	–	–	1	2	4	8
Sir Charles	–	–	–	–	–	–	1	2	4	8
Mary Lowndes	–	–	–	–	–	–	1	2	4	8
Victor	–	–	–	–	–	–	1	2	4	8
Potomac	–	–	–	–	–	–	–	1	2	4
Splendid	–	–	–	–	–	–	–	1	2	4
Saturn	–	–	–	–	–	–	–	1	2	4
Saturn	–	–	–	–	–	–	–	1	2	4
Rhea	–	–	–	–	–	–	–	1	2	4
Countess	–	–	–	–	–	–	–	1	2	4
Dick Swiveller, Jr	–	–	–	–	–	–	–	1	2	4
Countess	–	–	–	–	–	–	–	–	1	2
Taintor	–	–	–	–	–	–	–	–	1	2
Comus	–	–	–	–	–	–	–	–	1	2
Comus	–	–	–	–	–	–	–	–	1	2
St. Clement	–	–	–	–	–	–	–	–	1	2
Major	–	–	–	–	–	–	–	–	1	2
Czar	–	–	–	–	–	–	–	–	1	2
Countess	–	–	–	–	–	–	–	–	1	2
Dick Swiveller	–	–	–	–	–	–	–	–	1	2
Dove	–	–	–	–	–	–	–	–	1	2
Diana	–	–	–	–	–	–	–	–	–	1
Custard	–	–	–	–	–	–	–	–	–	1
Priuce John	–	–	–	–	–	–	–	–	–	1
Splendens	–	–	–	–	–	–	–	–	–	1
Totals	1	2	7	16	41	92	191	389	788	1,580

or heterozygous condition). The meaning here will be clear if a concrete example is considered. When one brother and sister mating is made 50 percent of the maximum possible number of different ancestors is eliminated. It is at least readily conceiv-

able, if indeed it cannot be said to be highly probable, that no two individuals among higher animals and plants are *exactly* alike in zygotic constitution when *all* hereditary characters are taken into account. This means, in last analysis, that each individual must differ from every other by at least one unit factor, possibly more. Once mating of brother and sister will diminish the number of such differences by 50 percent from what it would have been had no such mating occurred. The number of homozygous individuals *with respect to the hereditary differences remaining,* however, will not increase. This is practically equivalent to saying that while self-fertilization increases the proportion of *individuals* homozygous with reference to all characters, the closest inbreeding other than self-fertilization, if continued, increases the proportion of *characters* with respect to which all individuals are homozygous. Thus while both processes tend towards uniformity in the progeny, it is a different kind of uniformity obtained in a different way, in the one case from what it is in the other.

While in the above discussion only brother × sister mating is mentioned it is clear that the same reasoning applies regarding the meaning of the coefficients of inbreeding in all other types of mating.

There are other theoretical relations of inbreeding coefficients which are of interest, but to discuss them in detail here is not possible.

Concluding Remarks.

In this paper has been presented in abstract a general method of measuring the intensity or degree of the inbreeding practised in any particular case. The method proposed is shown to be perfectly general. It is based on no assumption whatever as to the nature of the hereditary process. On the contrary it is founded on the most completely logical and comprehensive definition of the concept of inbreeding that it seems possible to formulate. This is, in simplest form, that the most fundamental objective criterion which distinguishes an inbred individual from one not inbred is that the former has fewer different ancestors than the latter. It is believed that the proposed coefficients of inbreeding may be made extremely useful in studies of the problem of the effect of inbreeding, whether in

relation to its purely theoretical aspects, or in the practical fields of stock-breeding and eugenics.

Table Showing the Maximum Possible Number of Different Ancestors in the First Twenty Ancestral Generations (Obligate Bisexual Reproduction).

Ancestral Generation.	Maximum Possible Number of Ancestors.	Ancestral Generation.	Maximum Possible Number of Ancestors.
1	2	11	2,048
2	4	12	4,096
3	8	13	8,192
4	16	14	16,384
5	32	15	32,768
6	64	16	65,536
7	128	17	131,072
8	256	18	262,144
9	512	19	524,288
10	1,024	20	1,048,576